STUDIES ON SECOTIACEOUS FUNGI VII. SECOTIUM AND NEOSECOTIUM.

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We have had occasion to mention the genus *Secotium* in the narrower sense as based on *Secotium gueinzii* Kunze from South Africa. These references to *S. gueinzii* in the preceding parts of our studies on secotiaceous fungi were motivated by the necessity of comparing the characters of the type species of the genus with the characters of the other genera of the family as proposed in our previous papers.

We have now arrived at the question: what is the position of *Secotium gueinzii,* and which other species of *Secotium* are close to it?

In the first place we wish to redescribe the species to facilitate the comparison.

Secotium Kunze, Flora 23:321. 1840.

Secotium gueinzii Kunze, l.c. p. 322.

Gastrocarp convex, truncate below or not, always deeply sinuate underneath along the apex of the stipe (like *Endoptychum depressum*), semiglobose to campanulate, 30–60 mm. broad, about 32–42 mm. tall.

Peridium (inner) tessellate (with canal-like depressions), not gelatinized, white-buff (dried fuscidulous-yellowish), sometimes covering the gleba completely, sometimes pulled back (down) to expose some part of gleba; gleba loculate, with small chambers which do not show lamellar arrangement in any form but are winding, irregular, and unequal, not pulverulent, the walls white, thin, ochraceous buff to light brownish and said to have been pale olive, the exposed surface of gleba (if any) vertically surrounding the apex of the stipe.

Stipe up to 70 mm. long and 5–10 mm. broad at apex, up to 22 mm. broad at base, buffish colored, apparently smooth and glabrous, dry, stuffed; columella continuous with the stipe and either percurrent or not, if not, then sending out tramal plates with thick branches which merge with the normal thin tramal plates making up the loculi, at times changing direction in relation to the stipe and becoming oblique rather than vertical, broadened into the upper portion of the peridium if percurrent, white; volva said to be present, whitish, eventually disappearing except at the base of the stipe where it appears cothurnate, a distinct annular veil such as seen in *Endoptychum depressum* not described, not seen in the fragments available, and not clearly shown in illustrations. Context white, dry-fleshy, probably when fresh somewhat like *Endoptychum agaricoides*.

Spores (8.5–) 11–14 × (6.3–) 8.2–9.7μ, short ellipsoid but ovate in frontal view, somewhat inequilateral in profile (asymmetric), with oblique eccentric sterigmal appendage, pale olive-melleous to melleous-

[1] Papers from the University of Michigan Herbarium and the Department of Botany, No. 1087, University of Michigan, Ann Arbor, Michigan.

hyaline, the wall thick and complex (at least four wall-layers discernible), smooth, some with an apical germ pore, or some with an apical truncation but without a demonstrable discontinuity in the wall (or else pore incomplete and spore not truncate), slightly metachromatic in cresyl blue but absorption of the cresyl blue very variable, if weakly stained, a lilac line along the endosporium visible and inner two layers sometimes remaining incolorous, when strongly stained the whole wall and interior deep blue as in spores of *Chlorophyllum molybdites,* correspondingly, with Melzer's reagent distinctly pseudoamyloid but some remaining inamyloid and a few discoloring only partly; not forming a pulverulent mass in the gleba.

Basidia about 28 × 9.7μ, 4-spored, sterigmata variable, some thin and straight but oblique, some thin and slightly curved (somewhat intermediate between "agaricoid" and "gastroid"); cystidia not seen, but yellow "Pollinarien" described and illustrated by Corda.

Trama hyphous throughout, in places very slightly gelatinized, hyaline, in peridium extremely irregular but more radially arranged in outermost layer of endoperidium, the hyphae of all layers 2–6 μ in diam., inamyloid and with clamp connections.

Terrestrial on the sand steppes of the Cape of Good Hope, South Africa, Uitenhage, fruiting in summer (December). Leg. *Queinzius,* comm. M. C. Cooke (NY, part of type).

Another part of the type is at Kew (Singer has seen but not studied it, but he is certain that it is part of the same collection, which is corroborated by the fact that what little Heim communicates about the "Berkeley-type" coincides well with our findings). It is possible that part of this was also in Corda's Herbarium which is in Prague.

This species has the same essential spore-wall characters as *Endoptychum agaricoides* and *E. arizonicum,* namely the pseudoamyloid reaction, the thick, many-layered wall, and the relatively light color (varying to hyaline). In spite of these similarities, there are important differences such as the presence of a volva, non-pulverulent gleba, abundant clamp connections, and large ellipsoid spores with a germ pore. In view of these differences it appears illogical to us to place *S. gueinzii* in the same genus with *Endoptychum.* This was apparently also Zeller's point of view.

However, two other species, intermediate in their characters, need to be considered here. One is *Secotium macrosporum* Lloyd. It is intermediate in such basic characters as the pulverulent gleba and degree to which clamps are present, but is strikingly distinct because of the complex ornamentation of the spores. With some modifications the spore ornamentation is the type that is found in some tropical Lepiotas (*Leucoagaricus*) and/or (this is significant), in the Lycoperdaceae. We shall discuss the affinities of this interesting species later, but considering its differences from both *Endoptychum* and *Secotium,* we cannot convince ourselves that according to any generic concept short of re-establishing *Secotium sensu lato,* can *S. macrosporum* be considered congeneric with either *Secotium* or *Endoptychum.*

This establishes *Secotium* as a monotypic genus, and necessitates establishing a new genus for *S. macrosporum*. We propose for it the new generic name *Neosecotium,* this being a New World *Secotium* and a species only now critically analyzed (Neo—new; secotium—a loculate system).

Neosecotium gen nov.

Carpophoris haud volvatis, pallidis, stipitatis, columella percurrente; gleba demum paulum vel manifeste pulveracea; sporis hyalinis leviter ochrascentibus, pseudoamyloideis, poro germinativo instructis, globosis, membrana admodum crassa reticulatim fracta ornamentatis; fibulis praesentibus sed sparsis.

Typus generis: *Secotium macrosporum* Lloyd.

Neosecotium macrosporum (Lloyd) Sing. & Smith, comb. nov. *Secotium macrosporum* Lloyd, Mycol. Writ. 1:139. 1903.

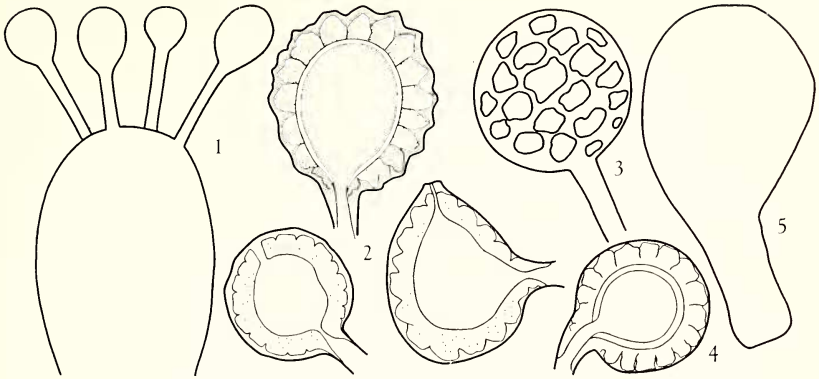
Gastrocary 1–3 cm. high and 1–2 cm. thick, subelliptic to nearly globose, the margin not separating from the stipe-columella.

Peridium smooth, avellaneous or paler, the lower portion whitish-pallid at times.

Gleba chambered at first, but somewhat pulverulent and at maturity little if any structure visible, in immature stages showing chambers oriented in an obscure lamellar orientation, about wood brown (R) near maturity or finally becoming more cinnamon, not separated from columella.

Stipe-columella percurrent, pallid throughout as dried, 2–3.5 mm. diam. in widest place (as dried), very little (2–3 mm.) projecting below the gastrocarp as a stipe.

Spores globose and 13.5–18 μ or 14–18 × 12–15 μ and subglobose to slightly ovate, ochraceous to tawny in KOH (depending on degree of maturity), dark red-brown in Melzer's solution (pseudoamyloid), with a short to rather long sterigmal appendage as in many Lycoperdaceae, the pedicel hyaline and thin-walled except for the area where the thickening of the spore wall projects down into it slightly, centrally attached or rarely slightly eccentric; spore wall complex, at maturity with a thin hyaline perisporium which adapts itself to the configuration of the wall beneath (exosporium and possibly endosporium combined); exosporium and endosporium together 3–5 μ thick, rusty brown in KOH at maturity but nearly hyaline earlier, deep red-brown in Melzer's solution, smooth at first but soon becoming cracked into an areolate pattern and the fissures gradually deepening to produce a warty to almost echinulate effect and at this time the spore surface appearing distinctly roughened, but perisporial membrane still visible over warts and depressed into the crevices, in young stages where the inner thick wall is still hyaline an apical germ pore can be observed in some spores, and in abnormal spores a lateral beak furnished with a distinct pore is clearly evident, the pore obscured in old spores by the cracking up of the thick inner layer of the wall.



FIGS. 1–5. *Neosecotium macrosporium*: 1, upper part of basidium showing tubular sterigmata and young spores, × 450; 2, mature spores in optical section, × 1000; 3, surface view of nearly mature spores, × 1000; 4, optical section of immature spores, × 1000; 5, young basidium, × 450.

Basidia large, 25–37 × 14–17.5 μ, clavate to subelliptic-pedicellate, thin-walled and hyaline or the wall slightly thickened and brownish—hence the cell more persistent than usual; sterigmata typically 4 and tubular, not often tapering appreciably and the young spore acropetally attached or very rarely appearing slightly eccentric. Cystidia, none observed.

Subhymenium of broad intricately interwoven hyphae, hence in section appearing somewhat cellular from cut hyphal ends; hyphae of the peridium filamentous, many hyphal cells somewhat to markedly inflated (4–12–18 μ in diam.), the outer layer more or less radially arranged and melleous to dingy ochraceous in KOH, gradually paler toward gleba, not at all gelatinous or toward gleba only sub- gelatinous (slightly translucent in KOH); clamp connections absent to rarely present.

The type was collected near Dallas, Texas, by E. P. Ely. The best material we have seen, however, is a collection by R. Sprague, June 13, 1941, in grass plots on sandy soil at Mandan, North Dakota (NY).

This is a most interesting species in many respects: the long, tubular sterigmata which often break off leaving the upper half attached to the spore as a pedicel or appendage, the tendency of the gleba to become powdery at maturity, and the type of spore ornamentation in mature spores are all strongly reminiscent of the Lycoperdaceae, so much so, in fact, that we are inclined to believe that *N. macrosporum* actually does represent a true link connecting the Secotiaceae to that group. The outer surface of the dried peridium is almost Calvatia-like in texture, but this, of course, may not have any phylogenetic significance beyond that indicated by the type and arrangement of the hyphae of the outer zone of the peridium.

The pallid to avellaneous tone of the mature gastrocarp and its texture are also reminiscent of *Lepiota naucina*. Actually, aside from the shape

of the spore and the peculiar way in which the inner wall layers break up, the spores themselves show resemblances to those of *Macrolepiota* and *Leucoagaricus* by the presence of a germ pore (though it is obscured at maturity) and the strong pseudoamyloid reaction of the thick inner wall. Also the spores are metachromatic in Cresyl blue—at least the pale colored spores are. These characters appear to us to connect *Neosecotium macrosporum* to the Agaricales, family Agaricaceae sensu Singer, and very likely in the vicinity of *Chlorophyllum* and *Macrolepiota*. Hence we have here a connecting link, as we see it, between the Lycoperdaceae on the one hand and a family of agarics on the other.

As far as we are aware, this is a heretofore unsuspected connection between the two groups, and when viewed in this way it is cause for much interesting speculation on the course which evolution has followed. Since in this series of papers we are not discussing the direction of evolution, we shall limit ourselves to considerations which we believe to be based on facts as follows:

The lycoperdaceous fungi show a wide range of spore color just as does the family Agaricaceae, and, though the spores in the Lycoperdaceae are small, many show a sufficiently similar type of ornamentation to make it imperative that spore structure in that order now be studied by the techniques in use for the study of spores in the Agaricales.

The problem of the powdery gleba in the Lycoperdaceae is now no problem at all as far as its being an obstacle to ascertaining connections to the Agaricales. In a number of species of *Agaricus* the gills become very soft and almost collapse after maturity, and in carpophores which did not open but which dried out *in situ* it is a simple matter to understand how these structures could break down to a powdery consistency. The presence of a highly developed capillitium is certainly to be regarded as an advanced character in the Lycoperdaceae, but this, no matter from which source one derives the Lycoperdaceae—the agarics or lower Gastromycetes—does not offer any serious hurdle to establishing relationships in either direction. Any hymenophoral trama with thick-walled hyphae could easily give rise to "capillitium" if the remaining trama consisted of thin-walled perishable hyphae. There is no reason why thick-walled hyphae should not appear "de nova" in the glebal trama of Gastromycetes in more than one evolutionary series, since wall-thickenings of hyphae are one of the commonest types of hyphal adaptation in the fungi as a whole.

The second species of *Neosecotium* was found among the collections of *Arcangelliella* in the Zeller Herbarium. A redescription of it follows:

Neosecotium africanum (Lloyd) comb. nov. *Octaviania africana* Lloyd, Myc. Writings 7:1142. 1922. *Octaviania africana* Verwoerd, S. Afr. Journ. Sci. 22:164. 1925. *Arcangeliella africana* (Lloyd) Zeller & Dodge, Ann. Mo. Bot. 22:365. 1935.

Fructifications spherical, 10–15 mm. thick, drying cinnamon-brown to

TABLE 1. COMPARATIVE FEATURES INDICATING INTERMEDIATE POSITION OF NEOSECOTIUM MACROSPORUM BETWEEN ENDOPTYCHUM ARIZONICUM AND SECOTIUM GUEINZII.

	Endoptychum arizonicum	*Neosecotium macrosporum (Secotium macrosporum)*	*Secotium gueinzii*
SEPTA	without clamp connections	some with, some without clamps	with clamp connections
VOLVA	none	none	present
PERIDIAL SURFACE	rough but not tessellate	smooth	tesselate
GLEBA	pulverulent (strongly)	pulverulent (moderately)	non-pulverulent
SPORES			
ORNAMENT	smooth	ornamented	smooth
SIZE	small	large	large
SHAPE	subglobose	globose	ellipsoid
PORE	none	present	present

Dresden brown; peridium hard, duplex, the outer layer 140–160 μ thick, composed of closely woven slender, hyaline hyphae 1.5–2 μ in diam., the inner layer 375–400 μ thick, composed of hyaline, more loosely woven septate hyphae 3–4 μ in diam., "with lactiferous ducts" . . . . Zeller & Dodge, separable; gleba drying from ferruginous to snuff brown; tramal plates 15–30 μ thick; basidia clavate, 23–30 × 7–8 μ, sterigmata 10–15 μ long and filiform.

Spores (giant spores) 17–20 × 14–16 μ, "normal" spores 13–15 × 10–13 μ, subglobose to broadly ellipsoid; sterigmal appendage pedicellate; dingy yellowish in KOH, *dark red-brown* in Melzer's reagent (pseudoamyloid); ornamented and thick-walled, inner wall about 2 μ thick, outer wall broken up into a pattern of broad obtuse to flattened warts due to the cracking of the wall; no germ pore found.

The description of the spores was taken from the part of the type in the Zeller Collections of the New York Botanical Garden. The hymenium and tissues of the fruiting body failed to revive sufficiently for critical study. It is more than evident to us that because of the pseudoamyloid spores with their characteristic ornamentation the species belongs in *Neosecotium* even though in the material available we failed to establish the presence of a germ pore. The hard, brown peridium should amply distinguish *N. africanum* from *N. macrosporum*. From what we were able to ascertain from the limited material available, it appears to us that *N. africanum* is more gastroid than *N. macrosporum*, in fact may represent a distinct genus at the level of *Martellia*. Because it represents a different level of evolution, it is not included in the chart with the other distinctly secotiaceous species.

Naturally, the genera *Endoptychum*, *Neosecotium*, and *Secotium* form a definitely circumscribed and sharply outlined group—a tribus or sub-

family—which may also contain such genera as *Polyplocium* Berk., *Gyrophrangmium* Mont., and *Longula* Zeller.

Since we do not wish to enter such intricate questions of purely gastromycete taxonomy as the possibility of maintaining all three last-named genera (which seem to us extremely close to each other), and since our experience with them is relatively limited, we prefer to omit these genera for the time being. However, their close relationship to *Secotium sensu stricto* as well as *Endoptychum* cannot be overlooked.

REVIEW

Comparative Morphology of Vascular Plants. By Adriance S. Foster, and Ernest M. Gifford, Jr. 555 pp., 213 figs. W. H. Freeman, San Francisco. 1959. $9.00.

The literature of vascular plant morphology has been greatly enriched by this new textbook by two prominent teachers and researchers at the University of California at Berkeley and Davis. In contrast with other morphology texts that have appeared in recent years, this is a product of men who have devoted their entire careers to the higher plants. As a result, the book is organized in a manner that emphasizes morphological problems of current interest in this area, with subdued treatment of the burning questions of morphology of the early years of this century that are currently only of historical interest. This book is likely to enjoy a long active life as a textbook and reference work, therefore a detailed review seems justified.

A unique feature that sets apart "Comparative Morphology" from earlier textbooks is the organization of material into two sections. In the first part, consisting of six chapters, the principal characteristics of the vascular plants are surveyed in a comparative fashion; in the second part individual chapters are devoted to treatments of the plant groups in systematic sequence. The classification system of Tippo is followed throughout. Extinct groups are treated in an integrated manner alongside their living relatives, but the emphasis is on modern plant types. Detailed descriptive material is not presented for its own sake, but rather as evidence for morphological or phylogenetic conclusions. The detail might be described as interpretative and illustrative rather than as encyclopedic.

The opening chapter tells the beginning student what morphology is all about. There is a discussion of the concept of homology, and of the kinds of morphological evidence that have proved most useful in reconstructing concepts of phylogeny, such as ontogeny, adult form, and the fossil record. The frontiers of modern experimental morphology and morphogenesis are described briefly and some pertinent unanswered questions are posed. The following chapter deals with the overall characteristics of the phylum of vascular plants, giving an outline of a typical life cycle involving an alternation of generations. The existence of apospory and apogamy and the significance of these phenomena on the classical theories regarding the origin of alternate generations is discussed. The phylum is then divided into the usual four subphyla of Eames and Tippo.

Four chapters dealing with the principal areas of morphological investigation are devoted to the vegetative sporophyte, the sporangia, the gametangia, and to embryogeny. Under the heading of vegetative sporophyte are included discussions of the general structure of shoot and root, types of branching, types of leaves, microphylls versus megaphylls, and the phylogenetic origin of leaves according to Bower. The Telome Theory is presented briefly. The area of plant anatomy is entered with a discussion of the problems of classification of tissues and tissue systems. The system of Sachs is presented, and the structure and development of the principal tissues are